OSCILLOSCOPIC AND STROBOSCOPIC ANALYSIS OF THE FLIGHT SOUNDS OF DROSOPHILA [1]

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The problem of the flight sounds of insects has recently been brought to focus in the admirable monograph of Sotavalta (1947). According to this author it was in 1866 that Mühlhäuser first suggested that "the pitch of the flight-tone was exclusively caused by the number of wing-strokes per second." By matching the tone of the flight sound with that of a suitable tuning fork, one should then be in a position to assign a corresponding frequency to the wingbeat itself. This possibility was exploited by Landois (1866) and became standard practice. Unfortunately, such a procedure is complicated by various difficulties, among which is the "soprano-tenor error" whereby the flight tone is matched with a tuning fork having twice the proper frequency (Sotavalta, 1947).

Sotavalta has revived the acoustic method with notable success. Endowed with "absolute pitch," this investigator has been able to dispense with apparatus and, by the direct use of his ears and musical training, to appraise the frequency of wingbeat of free-flying insects. Thus the flight sound of insects has become a matter of contemporary interest as a quantitative approach to the study of insect flight.

It is therefore surprising that the literature contains no adequate analysis of the flight sound of any insect or definite proof that acoustic studies record the same frequency of wingbeat as do more objective methods. As Chadwick (1939) has pointed out, "the relation between the pitch of an insect's tone and the frequency of its wing-motion is still not completely understood."

Solution of this problem depends on methods whereby measurements of both the flight sound and the frequency of wingbeat may be accomplished simultaneously on the same flying insect. This objective is well within reach of present methods. The electronic stroboscope, first applied by Chadwick (1939) to the study of insect flight, permits prompt and accurate measurements of the frequency of wingbeat. Concerning the flight tone itself, Davis and Fraenkel (1940) mention its measurement by the use of a microphone and cathode ray oscilloscope, and some preliminary application of this technique has also been described by Sotavalta (1947).

In the present investigation we have applied both the stroboscopic and oscilloscopic techniques to flying insects in an attempt to establish a direct correlation between the flight sound and the frequency of wingbeat.

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Material and Methods

Our first experiments were performed nine years ago on the fruitfly, *Drosophila funebris,* and the mosquito, *Culex pipiens.* Although the primary problems were solved at that time, the study has been recently repeated with improved techniques of sound recording. These latter studies have been performed solely on *Drosophila funebris.*

In brief, the tip of the abdomen of each fly was attached with melted paraffin to a small wire, according to a method described previously (Williams and Chadwick, 1943). The insect was then oriented 1.5 cm. in front of a Western Electric 640 AA condenser microphone. This assembly was located in a sound-proof room from which leads passed to an adjacent room housing the recording apparatus. The latter consisted of an oscilloscope of linear sweep characteristics used in conjunction with a preamplifier and a camera of stable, adjustable film speed. A check on film speed was provided by a neon light, placed in the field of the camera and driven by a half-rectified AC potential from an audio-oscillator. The recording system had an essentially flat response from a few cycles to 5000 cycles per second.

In addition to the insect, microphone, and switch for remote control of the camera, the first room also contained a General Radio "Strobotac" for independent measurement of wingbeat frequency by the stroboscopic method. In practice it was found that the noisy discharge of the stroboscopic tube interfered with the sound picture. In order to correlate the two types of measurement, the following procedure was adopted.

Flight was induced by a puff of air. The insect's performance was tracked with the stroboscope until the animal showed constant frequency of wingbeat. The stroboscope was then switched off, the camera started, and the sound picture recorded either on continuously moving film or in a number of consecutive sweeps of the oscilloscope. Flight was terminated by touching the animal's feet with a steel rod.

For the purpose of recording the sound picture from the outset to the termination of individual flights, stroboscopic measurements were discontinued, and the flight sounds recorded on continuously moving film.

Relation of Flight Sound to Wingbeat Frequency

Unlike the sound of a tuning fork, the buzz of a flying insect is by no means a pure tone. As shown in Figure 1, the exact character of the sound picture depends on the orientation of the insect with respect to the microphone. Though a sinusoidal waveform is never encountered, each orientation of the microphone yields a definite repeating pattern of fundamental wavelength.

In Table I wingbeat frequency has been estimated from the records in Figure 1 on the assumption that each repeating pattern corresponds to one cycle of wingbeat. The validity of this assumption is demonstrated by the excellent agreement between wingbeat frequencies in each flight as measured by oscilloscopic and stroboscopic techniques. This agreement persists when wingbeat frequency is increased by clipping the distal third from the tips of the wings.

These observations afford the first definite proof that, within the limits of experimental error, the fundamental frequency in the flight sound is the same as the frequency of wingbeat.

Details of the Sound Picture

As mentioned in the preceding section, the flight sound presents a waveform that depends on the orientation of the insect with respect to the microphone. In our oscilloscopic records, samples of which are illustrated in Figures 1 and 4, compression of air at the microphone is recorded as a downward deflection of the beam and rarefaction as an upward deflection. With the microphone anterior to the longitudinal axis of the insect, it will be observed in Figure 1 that the sound pattern is almost exactly the inverse of that recorded with the microphone posterior to the insect.

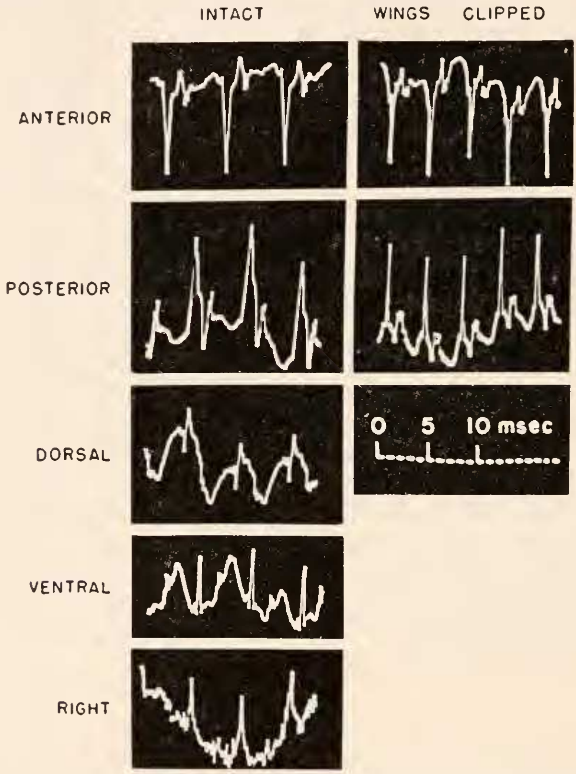

Figure 1. Sound produced by *Drosophila* during "fixed" flight. The orientation of the microphone with respect to the animal is stated at the left of each record. Compression of air at the microphone is recorded as a downward excursion. The records in the right hand column were obtained after clipping approximately one-third from the tips of the wings. Clipping the wings is seen to have little effect on the sound pattern despite the marked increase in wingbeat frequency.

As judged by its position when the insect is not flying, the baseline of zero change in air-pressure seems to lie approximately midway the vertical excursion of the oscilloscopic beam. Thus, as diagrammed in Figure 2, the microphone records a predominantly upward excursion or rarefaction anterior to the insect and a predomi-

Table I

Wingbeat frequency of Drosophila determined by oscilloscopic and stroboscopic techniques

	Sound frequency (beats/second)	Stroboscopic frequency (beats/second)
Intact insect:		
Head toward microphone	166	164
Abdominal end toward microphone	182	180
Dorsal side toward microphone	182	183
Ventral side toward microphone	182	186
Right side toward microphone	193	194
Wings clipped:		
Head toward microphone	250	247
Abdominal end toward microphone	270	261

nantly downward excursion or compression posteriorly. In terms of air flow this signals a net, polarized movement of air from front to rear (Demoll, 1918; Magnan, 1934).

Figure 2 attempts to correlate these pressure changes with the cycle of wingbeat. Whereas the latter is approximately equally divided into upbeat and downbeat (Magnan, 1934), the cycle of air-pressure is decidedly unsymmetrical. According to the analysis diagrammed in Figure 2, anterior rarefaction and posterior compression are present during approximately 85 per cent of each cycle of wingbeat. Only a small fraction of the wingbeat cycle, indicated by the spike in the records, produces anterior compression and posterior rarefaction. It seems necessary to conclude that polarized flow of air from front to rear is generated, not only by the downbeat of the wings, but also by a significant proportion of the upbeat.

Though the large and transient "spike" in each cycle of wingbeat cannot be accurately localized with the present data, we suspect that it corresponds to the

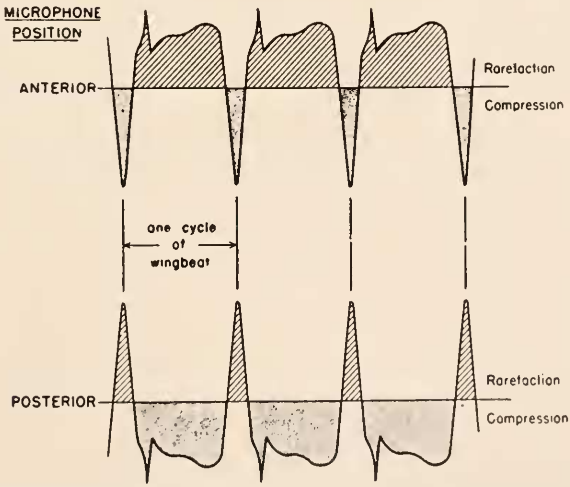

Figure 2. Correlation between the flight sound and the wingbeat. One cycle of sound corresponds to one cycle of wingbeat. For further explanation see text.

movement of the wings through the upper limits of their trajectory. This point could presumably be settled by studies in which the sound picture and the position of the wings were recorded simultaneously. Further study is also required to interpret the components of low amplitude that complicate the sound picture; especially is this true in regard to the rapid biphasic wave interpolated in each cycle of wingbeat (Fig. 2). Turbulences, movements of the thorax itself, and vibration of the halteres (at the same frequency but in opposite phase to that of the wings) are among the possible sources of such minor components.

Frequency of Wingbeat at the Outset and Termination of Flight

Unlike the stroboscopic method, the oscilloscope is able to track the rapid alterations in the frequency of wingbeat that occur at the outset and termination of flight. The behavior of wingbeat frequency under these conditions is recorded in Fig. 3. Two brief flights are plotted from beginning to end. In making the graphs, the total wingbeats were counted over 0.2-sec. intervals in the upper record, and over 0.5-sec. intervals in the lower one. These counts were then converted into beats per second in each case and plotted. Records of this type reveal that the early beats of the wings are accomplished at the high frequency characteristic of the entire flight.

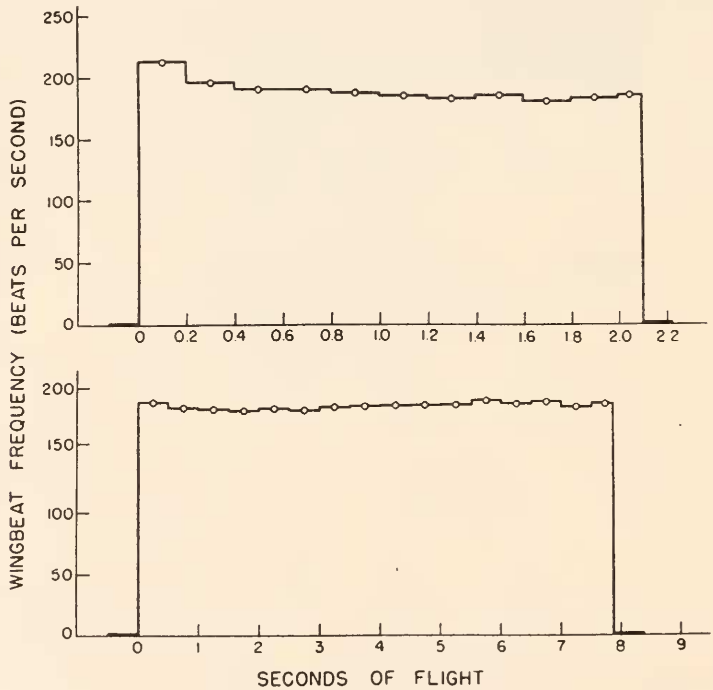

Figure 3. The frequency of wingbeat during a brief flight by each of two specimens. The frequency of wingbeat as determined from the sound records is seen to be approximately the same from the beginning to the end of each flight.

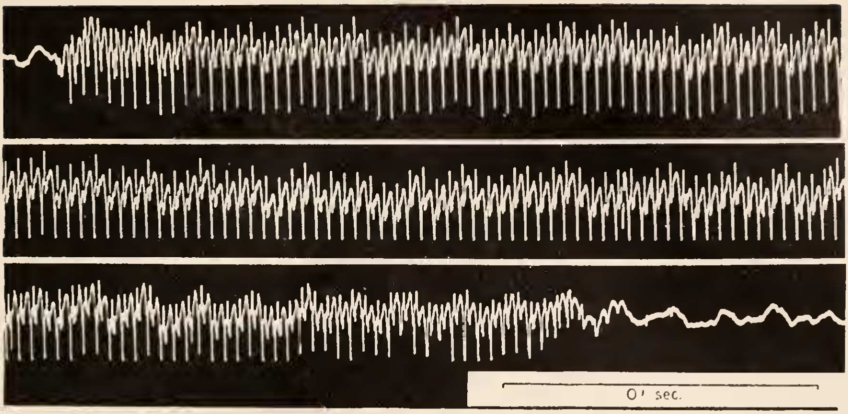

FIGURE 4. The beginning, middle, and end of a sound record of a specimen with clipped wings. The relative constancy of frequency of wingbeat, illustrated in Figure 3, is emphasized here. Irregularities at the end of the record are attributable to touching the insect with a steel rod for the purpose of terminating flight. The constant amplitude of the spikes in the middle record is an artifact due to the beam moving off the edge of the oscilloscope.

Figure 4 illustrates the sounds produced by an animal whose wings had been clipped. In this case 101 beats occur in the first 0.5 second as compared with 102 beats in the final 0.5 second. Again, the frequency of wingbeat is approximately constant from the beginning to the end of the brief flight.

DISCUSSION

Though the source of the flight sounds has long been a matter of controversy, there can be little doubt that in *Drosophila funebris* the bulk of the sound energy is the direct result of the movements of the wings. One cycle of wing motion corresponds to one cycle of flight sound. Consequently, the flight sound presents a waveform that reflects the underlying complexity of the wingbeat.

The waveforms pictured in Figure 1 are those of complex sounds. A "fundamental frequency" corresponding to the frequency of wingbeat is clear, but harmonics over a wide range are prominent and their relative strengths vary with the position of the microphone. These sounds obviously depart radically from the sinusoidal vibrations produced by tuning forks and oscillators. According to Miller and Taylor (1948), sounds very similar to these can, however, be perceived by some persons as having a pitch. The judgment is not easy to make and the accuracy with which the pure tone is matched to the complex sound is poor at best. In these facts may lie some of the subjective difficulty experienced in matching the buzz of an insect to a pure tone. Furthermore, when subjects are required to match a complex sound and a tone, a common error is to select a tone of about twice the "fundamental frequency" of the complex sound (Miller, 1950). This fact, along with the "soprano-tenor" error cited earlier, may help account for the tendency to report, from subjective flight-sound data, wing beat frequencies approximating twice the actual number (see Sotavalta, 1947, pp. 16–21). Finally, the demonstrated complexity of the insect sound should make clear the difficulties inherent in attempts to duplicate insect sounds by generating pure tones with an oscillator or tuning fork (Roth, 1948).

Analysis of the waveform, as in Figure 2, suggests that there is remarkable aerodynamic efficiency in the total cycle of wingbeat. The insect is apparently able to extract useful flight energy, not only from the downbeat of the wings, but also from the upbeat. Approximately 85 per cent of the cycle of wing motion makes positive contribution to flight; less than one-fifth of the wingbeat cycle seems to make negative contribution to the effective, polarized flow of air produced by the beating wings.

In addition to these points of interest to the aerodynamics of insect flight, the sound picture also provides useful information concerning the underlying neuromuscular mechanism. Figures 3 and 4 illustrate that during brief flights the initial and final beats of the wings are performed at the characteristic high frequency. Evidently, the mechanism that regulates the tempo of wingbeat must be fully functional at the very outset of flight.

This observation is pertinent to a theory recently proposed by Pringle (1949) to account for the unusual physiological properties of the flight muscles of flies. According to this theory,the principal features of which have been confirmed by Roeder (1950), the movement of the wings in dipterous insects depends on a remarkable myogenic mechanism. Under the general excitatory influence of the nervous system, the muscles serving the downbeat contract when stretched by the antagonistic muscles serving the upbeat. A continuation of this process leads to movement of the wings at a tempo determined largely by the loading of the flight muscles and thus, indirectly, of the wings.

Since the wing loading, under otherwise constant conditions, is fixed largely by anatomical factors, the theory would predict that the initial wingbeat be executed at the ultimate frequency. In this respect Pringle's new theory finds confirmation in the results of the present investigation.

Summary

1. Oscillographic records are presented of the sounds produced by *Drosophila funebris* during "fixed" flight. Stroboscopic determinations of wingbeat frequency indicate that one cycle of wing motion corresponds to one cycle of flight sound.

2. The sounds generated during flight are complex and radically different from the simple harmonic motion of a tuning fork. Certain consequences of this fact are discussed.

3. Analysis of these sounds suggests a remarkable aerodynamic efficiency for the wingbeat cycle. The flying insect produces a polarized flow of air from front to rear during approximately 85 per cent of the wingbeat cycle.

4. During brief periods of flight the first few and the last few beats of the wings are accomplished at the high frequency characteristic of the entire flight. This fact is considered in relation to Pringle's new observations concerning the neuromuscular system of dipterous insects.

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